Patterns of Suspension Feeding in the Freshwater Bryozoan *Plumatella repens*

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Abstract. Feeding of large and small colonies of *Plumatella repens* was assessed under two flow conditions. Large colonies ingested greater numbers of particles than small colonies and feeding of colonies of both sizes increased with flow. However, the rate of increase depended on colony size. Small colonies increased feeding to a greater degree than large colonies. Mechanisms that may explain these patterns are discussed. These results contrast with an earlier study of feeding in a freshwater bryozoan. The conflicting results may reflect experimental conditions. In the previous study a small volume of still water likely entailed greater food depletion by large colonies. In our study food depletion did not occur and ambient flow carried away filtered water. We discuss how the relatively large, U–shaped lophophores of freshwater bryozoans function to produce powerful feeding currents that are suited to feeding in lotic and lentic habitats.

Introduction

Assemblages of colonial suspension feeders are common to both marine and freshwater habitats. In general, marine assemblages are characterized by high levels of competition for space and food as asexual growth results in numerous interactions (*e.g.,* Stebbing, 1973; Jackson, 1979; Buss, 1980; Kay and Keough, 1981; Rubin, 1982; Okamura, 1988; López Gappa, 1989). By contrast, very little is known about the dynamics of freshwater systems where assemblages of colonial invertebrates such as bryozoans and sponges are common (Bushnell, 1966; Wood, 1973; Frost, 1991; Karlson, 1991; Ricciardi and Lewis, 1991). However, competition for food and space has been shown to influence patterns of distribution and abundance of freshwater insects (*e.g.,* Hildrew and Townsend, 1980;

McAuliffe, 1984; Hart, 1985; Chance and Craig, 1986; Lamberti *et al.,* 1987; Ciborowski and Craig, 1989).

Investigations of marine bryozoans have revealed that colony size, neighbors, and ambient flow conditions can influence feeding success (Buss, 1980; Okamura, 1984, 1985, 1988) and subsequent colony growth (Okamura, 1992). Thus patterns of suspension feeding play an important role in the dynamics of these assemblages that are typically limited by space. Unlike their marine counterparts who feed with a circular lophophore (an apical tentacular crown), freshwater bryozoans (Cl: Phylactolaemata) possess a relatively larger and U-shaped lophophore. However, little is known about comparative patterns of feeding in freshwater bryozoans and how these may influence patterns of distribution and abundance of freshwater populations. For these reasons we undertook to characterize how colony size and ambient flow conditions influence suspension feeding in the freshwater bryozoan *Plumatella repens.*

Materials and Methods

Plumatella repens is probably the most common freshwater bryozoan and shows a cosmopolitan distribution (Wood, 1989). As its name implies, colonies are repent, adhering to the substratum as a series of branching zooecial tubes that can spread to cover large areas. Lophophores typically are deployed some distance apart as a result of elongation of zooecial tubes. Colonies are found in lakes, ponds, and streams on a variety of substrata including the undersurfaces of aquatic vegetation (especially lily pads: pers. obs.), submerged branches and roots, and rocks and stones (Wood, 1989).

Colonies for feeding studies were collected from a 47-year-old gravel pit located at Cassington Nurseries in Cassington, Oxfordshire. Pieces of lily pads containing large

(5–7 cm in diameter) and small (2–3 cm in diameter) colonies were brought to the laboratory where feeding studies were conducted. Lily pads were cut to approximately equal sizes for each treatment (7 cm for large colonies and 5 cm for small colonies; colonies were located centrally).

During feeding trials, cut lily pads containing colonies were floated on the surface of the water in the working area of a recirculating flow tank that contained a suspension of polystyrene particles. Lily pad segments were retained in position with thin lengths of wire. Colonies on the undersurfaces of the lily pads were thus immersed just below the surface of the water as they are in the field.

Polystyrene particles were suspended in distilled water at a concentration of 200 particles $\cdot$ ml^{-1} (SD = 3.95, n = 10). The concentration of particles was estimated by counting 10 haphazardly chosen fields of 10 samples of suspension. Polystyrene particles have been used to study feeding in marine bryozoans (*e.g.*, Okamura, 1984, 1985), and preliminary investigation revealed *Plumatella* would ingest them in large numbers. The diameter of the particles was 19.1 μm (SD = 0.6 μm) (Duke Scientific Corporation, Palo Alto, California) and lies within the size range of normal food items ingested by *Plumatella* (Kaminski, 1984). The concentration of particles was well within the range experienced by suspension feeders in their natural environment (DeMott, 1986).

Two standard flow conditions were created by effecting two known velocities in the mid–channel section of the flow tank (approx. 3–10 cm below the air-water interface, 2 cm in from the sides of the flow tank, and 20 cm long) (total cross section of water in the flow tank was 15 $\times$ 17 cm) during feeding trials. In the slower flow condition, velocity in the mid–channel section was 2.5 cm $\cdot$ s^{-1} (SD = 0.40 cm $\cdot$ s^{-1}, n = 15), and in the faster flow condition it was 5.3 cm $\cdot$ s^{-1} (SD = 0.80 cm $\cdot$ s^{-1}, n = 15). These velocities were determined by timing the passage of particles (hydrated *Artemia* eggs) over a known distance (15 cm) of the mid–channel section. Since lily pads with colonies were floated on the surface of the water, interaction of flow with the air-water interface and with the lily pad substrata would have created a velocity gradient (a boundary layer) during feeding trials (Vogel, 1981). Thus colonies experienced slower ambient flow velocities than those measured at the mid-channel section. Although we did not have the means to characterize flow at the level of lophophores, casual observations indicated that colonies experienced qualitatively different flow conditions during the feeding trials.

Colonies were starved for 24 h and then allowed to feed on particles for 10 min. Feeding trials of longer than 15 min were found to result in the ingestion of too many particles to assure accurate counting. A feeding trial time of 10 min is shorter than the gut passage time of various marine bryozoans (Winston, 1977). As the polystyrene particles were slightly denser than freshwater, a poultry baster was used at two minute intervals to resuspend particles. Immediately after each feeding run, colonies were placed facing down in individual petri dishes containing distilled water. Feces obtained after 12 h were collected and preserved in 80% ethanol until sampling.

Feeding rates were estimated by determining the mean number of particles per fecal pellet. Individual fecal pellets were gently squashed under a cover slip on a microscope slide, and the number of particles was counted using a compound microscope. Forty fecal pellets were sampled per colony when colonies produced large numbers of fecal pellets, otherwise all fecal pellets were sampled. As the relative proportions of actively feeding zooids varied in colonies during feeding trials, the total number of pellets produced per colony is not particularly informative. However, to check that fecal pellets did not vary with colony size, the maximum lengths and widths of 3–5 fecal pellets of large (n = 17) and small (n = 8) colonies were determined (colonies were not used in feeding trials).

Data on mean number of particles per fecal pellet per colony in the different treatments and on fecal pellet size were checked for normality and heterogeneity of variances prior to analysis. F-max tests revealed heterogeneous variances in the number of particles per fecal pellet per colony so data were log-transformed for ANOVA.

Results

Zooids of phylactolaemates produce mucus-encased fecal pellets that appear to be of fairly fixed sizes and regular shapes. Observations suggest that pellet dimensions reflect the dimensions of the packaging region of the hindgut (Okamura, pers. obs.). Data on fecal pellet size collected for small and large colonies support these observations. The mean volume of fecal pellets did not vary with colony size (mean volume of fecal pellets for large colonies was 3.24×10^{-3} mm^3 [SD = 1.8×10^{-3}] and for small colonies was 4.38×10^{-3} mm^3 [SD = 2.67×10^{-3}]; t = 1.264, df = 23, P = 0.219). Furthermore, although the total number of fecal pellets produced by colonies was not determined (since the number of feeding zooids per colony was variable and very difficult to count during feeding trials), fecal pellet production during experiments seemed generally to parallel feeding estimated by the number of particles per fecal pellet per colony. We therefore are confident that the data collected are good estimates of feeding rates.

Two-way ANOVA indicated significant size and flow effects on feeding (as measured by mean number of particles per fecal pellet per colony) (see Table I). The interaction of size and flow was also significant. These effects are shown in Figure 1. Large colonies had greater feeding

Source	df	Sum of squares	Mean square	F-value	P-value
Flow	1	1.169	1.169	42.690	0.0001
Size	1	1.820	1.820	66.457	0.0001
Flow × Size	1	0.400	0.400	14.592	0.0006
Residual	32	0.876	0.027		

rates, and feeding increased with flow in colonies of both sizes, however, when feeding from faster flow small colonies increased feeding rates approximately five times, while feeding rates of large colonies increased by a factor of only 1.8.

Discussion

Flow conditions and feeding

Increased feeding of *Plumatella* in conditions of greater flow contrasts with feeding patterns of marine bryozoans. In general, marine bryozoans experience reduced feeding success with increased ambient flow (*e.g.*, Okamura, 1984, 1985, 1988, 1990). The explanation for this difference may relate to the relative sizes and shapes of their lophophores. Phylactolaemate lophophores are large and U-shaped and have numerous ciliated tentacles. For instance, in *Plumatella repens* tentacle number ranges from 40–60 (Lacourt, 1968), while the number of tentacles in various marine bryozoan groups ranges from 8–34 (Winston, 1977). Best and Thorpe (1986) found that the strength of feeding currents related positively to lophophore size in marine bryozoans. This suggests that phylactolaemates should produce relatively more powerful feeding currents. Furthermore, deflection of lophophoral arms in phylactolaemates places cilia lining the arms in relatively closer proximity than the cilia that line the arms of the circular lophophores of marine bryozoans. This closer ciliary proximity should also contribute to creation of stronger feeding currents.

Bishop and Bahr (1973) report feeding currents extending 5 mm from lophophores of the phylactolaemate *Lophopodella carteri* (tentacle number = 50–95; Lacourt, 1968). McKinney *et al.* (1986) observed feeding currents to be effective at a distance of 3 mm in the marine cheilostome *Bugula neritina* (tentacle number = 23; Winston, 1978). (Both observations of feeding currents were in still water.) Greater pumping capacity of phylactolaemates may thus explain why, over the velocity range tested in this study, feeding by large lophophores of *Plumatella* was not constrained. Ultimately, of course, phylactolaemate feeding will be constrained by flow, when feeding currents can no longer overcome friction drag imposed by flow.

Greater feeding rates in the faster flow condition by *Plumatella* may reflect higher concentrations of particles in volumes of water diverted by feeding currents and, consequently, a greater flux of particles through the lophophore. Profiles of particle availability near surfaces can change: as flow increases higher particle concentrations and fluxes can occur closer to surfaces in boundary layer flows (Muschenheim, 1987; Fréchette *et al.*, 1989). Whether this is true for particle profiles near the air–water interface is not known to us (colonies floating on lily segments were situated just below this interface). Alternatively, there may be a greater propensity to feed at increased flow.

These results suggest that phylactolaemates possess powerful lophophores that allow them to feed from lotic and lentic environments (many, including *Plumatella*, occur in both). In diverting fluid from great distances, powerful lophophores may be significant for feeding in still conditions where food-depletion close to surfaces may be common and where lack of flow precludes resource renewal. Powerful lophophores will also be less overwhelmed by friction drag imposed by water moving downstream in lotic environments.

Colony size and feeding

The relatively high feeding rates of large *Plumatella* colonies may be explained by several mechanisms. The many lophophores of large colonies may concertedly pump greater volumes of water under varying flow conditions than can the fewer lophophores of small colonies (*i.e.*, the many lophophores of large colonies may concertedly produce a stronger pump). Alternatively, large
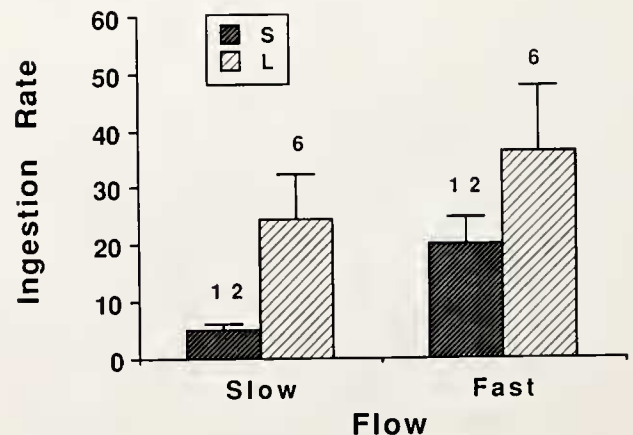

Figure 1. Ingestion rates (mean number of particles per fecal pellet per colony) of small (S) and large (L) colonies in slow and fast ambient flow (numbers above columns indicate number of colonies sampled). Bars represent two standard errors.

colonies may have relatively greater metabolic demands (possibly they invest more in statoblast or larval production per unit mass) than small colonies and therefore have a higher propensity to feed. However, the greater increase in the rate of feeding in small colonies with increased flow (by a factor of five) relative to large colonies (in which feeding increased by a factor of 1.8) (see Fig. 1) suggests that small colonies respond more strongly to increases in particle flux (or flow). Why small colonies should show such a marked response is not apparent. Perhaps small colonies create stronger ciliary currents in response to an abundance of food (particle flux serving as a cue) as has been observed in marine bryozoans (Best and Thorpe, 1983). Concerted pumping in large colonies may preclude the necessity to create individually stronger feeding currents and may provide for a more constant food supply.

Our results contrast with those obtained by Bishop and Bahr (1973) who found that clearance rates of the phylactolaemate *Lophopodella carteri* decreased with colony size. This discrepancy may relate, in part, to differences in colony morphology and growth in the two species, but it also is complicated by comparing feeding studies conducted under static and dynamic conditions and in dissimilar volumes of suspension.

Lophopodella is a higher phylactolaemate, producing gelatinous, globular colonies with no branching (Wood, 1991). Colonies of *Lophopodella* do not grow indefinitely but undergo fission, the resulting colonies slowly creeping apart. Fission in *Lophopodella* may result in avoidance of lophophoral feeding interference that occurs as colonies get bigger, hence maximizing filtering efficiency (Bishop and Bahr, 1973; Hughes, 1989). To some extent, our results for feeding in *Plumatella* support this contention. *Plumatella* does not undergo fission and its feeding does not decrease with increased colony size. The lack of interference in feeding in *Plumatella* may partly reflect its morphology. *Plumatella* colonies are tubular and branching and their lophophores are spaced much further apart than those of *Lophopodella*. However, we also believe it is crucial to consider differing patterns of excurrent flow and food depletion in our experiments and in those of Bishop and Bahr (1973).

In Bishop and Bahr's study (1973), *Lophopodella* colonies were placed in small vials (diameter = 22 mm) that contained 10 ml of an algal suspension. Thus colonies will have had ample opportunity to resample previously filtered water because the total volume of water was small and because, under conditions of still water, previously filtered water was not carried away. Thus, it is not surprising that clearance rates were lower for large colonies. The volume of suspension in our study was large (25 l), and food depletion was not significant. Furthermore, incorporation of ambient flow meant food–depleted water was carried away from colony surfaces.

Conclusion

This study indicates that feeding by freshwater bryozoans is less constrained by increased flow than it is in marine forms. As suggested above, the relatively large lophophores of phylactolaemates create powerful feeding currents that may be beneficial in both lotic and lentic environments. The complex hydrodynamics characteristic of marine habitats (see Denny, 1988) may ensure delivery of food to the level of small, circular lophophores of marine bryozoans. Furthermore, small, circular lophophores maximize the collective surface area for feeding, and colonies can benefit from the larger energy surplus associated with small size (Sebens, 1979, 1982; Ryland and Warner, 1986; Hughes, 1989). Thus lophophore size and shape in marine and freshwater bryozoans may reflect different solutions to different kinds of problems faced by small, colonial suspension feeders in the two sorts of environments. However, the role of phylogenetic constraint in determining lophophore morphology cannot be ruled out (traditional views hold U-shaped lophophores to be primitive). Although the majority of freshwater bryozoans possess large, U-shaped lophophores, small, circular lophophores are found in the phylactolaemate *Fredericella* and in the few gymnolaemates that have invaded freshwater habitats. These exceptions to the rule indicate that the significance of lophophore size and shape in freshwater habitats merits further investigation.

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